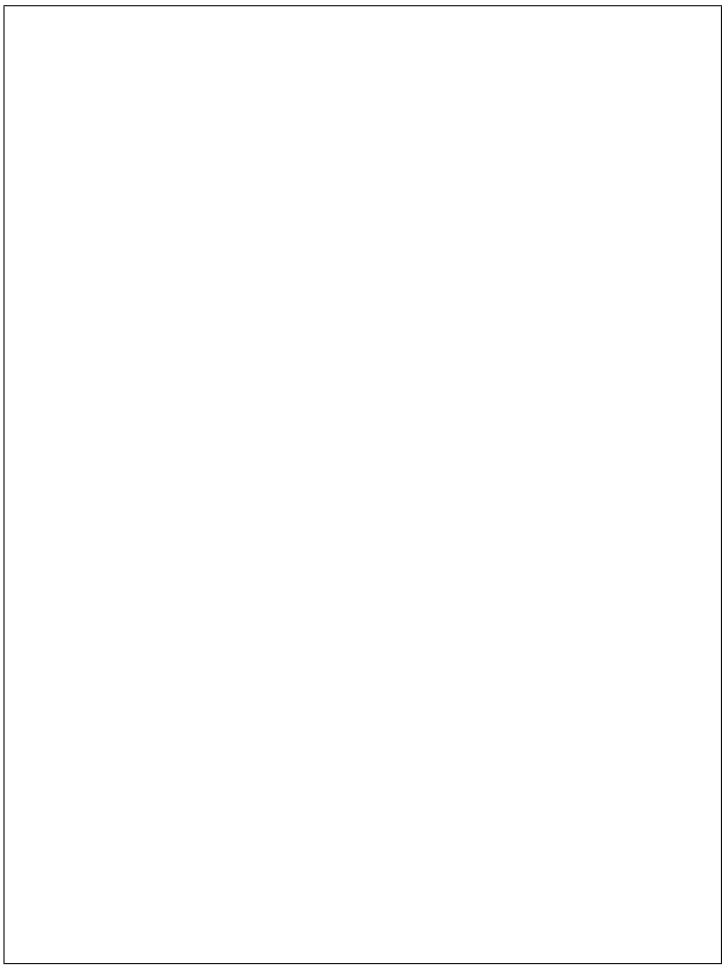

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Time course of amodal completion in face perception

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ABSTRACT

The visual system often automatically perceives partially occluded objects as whole and complete. This phenomenon is called amodal completion, but its mechanism is not fully understood. In the first experiment, we measured the psychophysical time course of face amodal completion using a performance-based method and found the amodal completion took place between 100 and 300 ms after stimulus onset. In the second experiment, we found the amodal completion could modulate event-related potentials (ERPs) in the same time range. These results provide further evidence regarding the representational development of occluded faces from local facial features to a coherent face.

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1. Introduction

Visual objects rarely occur in isolation in natural scenes. It is common for objects to occlude other objects or themselves in natural images. Although the sensory information specifying objects is optically incomplete due to occlusion, we have little difficulty completing occluded objects immediately and effortlessly, so that we see whole, uninterrupted objects. This perceptual filling-in of an occluded region of an object is known as amodal completion (Michotte, Thines, & Crabbe, 1964/1991).

Although it is possible that amodal completion could arise at a conceptual level, in the past few decades, many studies have demonstrated that amodal completion is an important visual process and it could profoundly influence performance in many visual tasks, including stereoacuity discrimination (Hou, Lu, Zhou, & Liu, 2006), texture segregation (He & Nakayama, 1994), visual search (Rauschenberger & Yantis, 2001), primed-matching (Sekuler & Palmer, 1992), shape perception (Ringach & Shapley, 1996; Shore & Enns, 1997), face recognition (Nakayama, Shimojo, & Silverman, 1989), visual pursuit (Stone, Beutter, & Lorenceau, 2000) and visual adaptation (Fang & He, 2005; Weisstein, Montalvo, & Ozog, 1972). In these studies, subjects' response to an occluded stimulus was more like to its complete counterpart than to its visible, unoccluded fragments. For example, Fang and He (2005) presented identical face fragments either behind or in front of a textured occluder as adapting stimuli. When the fragments were stereoscopically presented behind the occluder, they were amodally completed and organized into a coherent face by observers. When the same fragments were presented stereoscopically in front of the occluder, they were perceived as disjoint face fragments. This stereoscopic depth manipulation was originally devised by Nakayama and colleagues (1989) and sample stimuli are in Fig. 1. It was found that the former adapting stimulus (amodal completion) induced a significant face viewpoint aftereffect, similar to a complete face, but the latter stimulus did not.

Brain imaging studies also demonstrated that amodal completion occurs in the visual processing stream. Using functional magnetic resonance imaging (fMRI), Hegdé, Fang, Murray, and Kersten (2008) found that amodally completed objects activated the same cortical areas as their complete counterpart, including lateral occipital complex (LOC) and dorsal object-selective areas. With methods of high-density electrical mapping and inverse source estimation, Murray, Foxe, Javitt, and Foxe (2004) showed that the neural mechanism of amodal completion manifested as a modulation in response strength within high-level visual areas, including LOC and parietal structures, and the modulation took place as early as 140 ms after the stimulus onset.

Although previous studies have demonstrated the effect of amodal completion on various visual tasks and cortical activities, an open question is at what stage of the visual processing stream it is performed. For human subjects, measuring the time course of amodal completion using psychophysics, electroencephalogram (EEG) and magnetoencephalography (MEG) is a feasible way to address this question. Murray, Sekuler, and Bennett (2001) measured the extent of amodal completion as a function of stimulus duration over the range of 15–210 ms. Completion was assessed using a performance-based measure: a shape discrimination task that is

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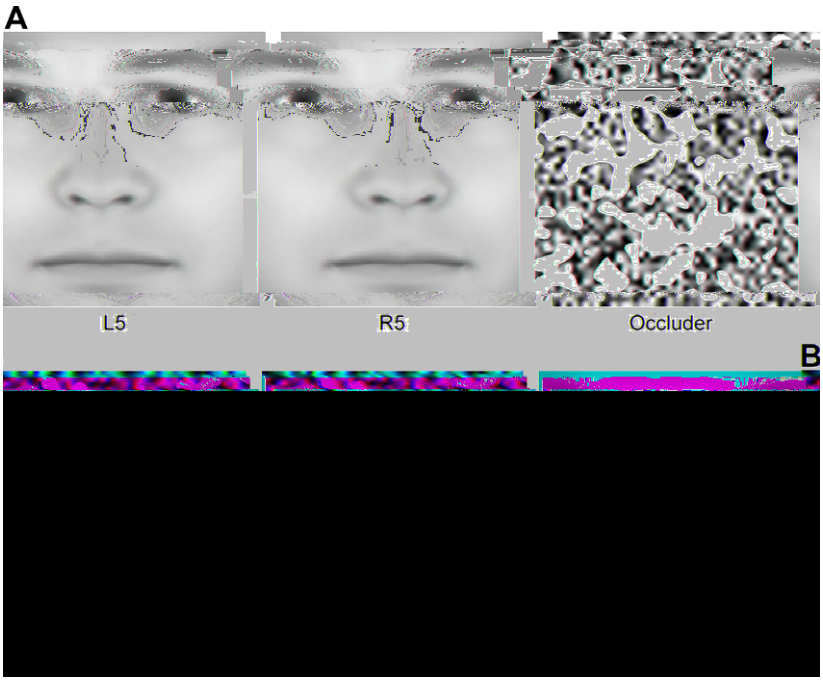

Fig. 1. (A) Sample images used to construct stimuli in the psychophysical and ERP experiments. The left and middle images are 5° side views of a face, which tilt to left or right, respectively. The right image is a textured occluder with irregular holes and (B) sample stimuli in the psychophysical and ERP experiments. They were generated by masking a face image with a textured occluder and were presented stereoscopically by using red/blue anaglyphic glasses. Disparity information specified that the occluder could be either in front of (left) or behind (middle) the face image. An isolated purple face (right) was also presented in the experiments.

easy if the stimulus is amodally completed and difficult if it is not. They found that amodal completion took about 75 ms to finish. Sekuler and Palmer (1992) used a primed-matching technique to examine the time course of amodal completion and their results suggested that amodal completion requires 100–200 ms. Johnson and Olshausen (2005) showed that the effect of amodal completion on object recognition can be seen with as little as 40 ms of stimulus presentation duration, however, the earliest ERP differences induced by amodal completion occur 130 ms after stimulus onset. On the other hand, Harris and Aguirre (2008) did not find the effect of face amodal completion on face-selective responses in MEG. The discrepancies between psychophysical time courses and the mismatch between psychophysical and electrophysiological time courses motivated us to carry out the current study.

In our study, the face stimuli – amodally completed faces and disjoint face fragments were similar to those in Fang and He (2005) and have been briefly described as above. In the first experiment, we adopted the performance-based measure developed by Murray et al. (2001) to unfold the psychophysical time course of face amodal completion. In the second experiment, we measured the ERPs induced by the face stimuli. We aimed to address several questions. How long must the visual system have access to the face stimuli to allow amodal completion to take effect? How is the effect of amodal completion reflected in the ERPs? Does the psychophysical time course closely match the electrophysiological one? The vast majority of previous amodal completion studies used simple shapes and line objects. However, face perception has been thought to involve specific cognitive and neural processes different from those that are used to recognize other shapes and objects (Kanwisher & Yovel, 2006, but see also Tarr & Cheng, 2003). To the best of our knowledge, no studies have been performed to investigate the time course of face amodal completion. Also, the electrophysiological time course might be especially of interest given the null effect of face amodal completion on MEG found by Harris and Aguirre (2008).

2. Methods

2.1. Participants

A total of 12 healthy subjects (five male and seven female) were involved in this study. Seven of them (three male and four female) participated in the psychophysical experiment and all of them participated in the ERP experiment. They were right-handed, had normal or corrected-to-normal vision, and no known neurological disorders. Ages ranged from 20 to 32. They gave written, informed consent in accordance with the procedures and protocols approved by the human subjects review committee of Peking University.

2.2. Apparatus and stimuli

In the psychophysical experiment, stimuli were presented on an Iiyama MM906UT 19 in. monitor, with a spatial resolution of 1024×768 and refresh rate of 100 Hz. The viewing distance was 86 cm. In the ERP experiment, stimuli were presented on an Iiyama MA203DTD 22 in. monitor, with a spatial resolution of 1024×768 and refresh rate of 100 Hz. The viewing distance was 100 cm.

Face stimuli in the psychophysical and ERP experiments were identical, which subtended $8.6° \times 8.6°$ of visual angle and were presented against a gray background. Occluded faces were generated by masking a 5° side view of a face with a textured occluder (Fig. 1A) and were presented stereoscopically by using red/blue anaglyphic glasses. About 35% of the face area was exposed to subjects through the holes of the occluder. Disparity information specified that the occluder could be either in front of or behind the face image (or face fragments) (Fig. 1B). Face fragments were always at zero disparity. The occluder was at either +0.12° or −0.12° of arc disparity. When the face fragments were stereoscopically presented behind the textured occluder (face behind occluder (FBO) condition), they were amodally completed and organized into a

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coherent face by observers. However, when the same fragments were presented stereoscopically in front of the textured occluder (face in front of occluder (FIO) condition), they were perceived as disjoint fragments. The FBO and FIO stimuli were identical in 2D, the key difference is the face amodal completion generated by the stereoscopic depth manipulation (Nakayama et al., 1989). In both experiments, complete faces without occlusion were also used (face only (FO) condition) and they were presented in purple (with only red and blue channels on) to match the color of the occluded faces.

The 5° side view of a face was generated by projecting a 3D face model with a 5° in-depth rotation angle onto the monitor plane with the front view as the initial position. Both left and right rotations were executed. The 3D face models were generated by FaceGen Modeller 3.1 (http://www.facegen.com/) and totally 20 models were used in this study. We generated 80 occluders, each of which has holes with different shapes. Any combination of face models and occluders was used for both the FBO and FIO conditions.

2.3. Experimental procedure

2.3.1. Psychophysical experiment

Each trial started with a 1000 ms blank interval. Then a face stimulus (FIO, FBO or FO) was presented at the center of the monitor with duration of 50, 100, 200, 300, 400 or 500 ms, followed by a 300 ms mask. The mask was generated by convolving a random noise pattern (pixel size = 0.23° × 0.23°) with a 2D Gaussian function (σ = 0.23°). Subjects pressed one of the two response keys to indicate the view direction of the face stimulus, either left or right (Fig. 2A). During the experimental period, a fixation point was presented at zero disparity and at the center of the monitor and subjects were required to maintain fixation.

There were totally 18 experimental conditions: six durations (50, 100, 200, 300, 400, and 500 ms) × three stimulus types (FIO, FBO and FO). The experiment consisted of eight sessions and a single session comprised six blocks of 60 trials. In each block, there were 20 trials for each of the three stimulus types and the stimulus duration was fixed. The order of six blocks (i.e. six durations) was randomized in a session. All data from eight sessions were pooled together for analysis.

2.3.2. ERP experiment

The experiment consisted of 16 blocks of 66 trials, including 20 trials for each of the three face stimulus types (FBO, FIO and FO) and six trials for a checkerboard stimulus. The checkerboard stimulus subtended the same visual angle as the face stimuli. In a trial, a stimulus was presented for 1000 ms and there was no mask. The inter-trial interval was randomized from 1000 to 1500 ms. Subjects were required to detect the presentation of the checkerboard stimulus by pressing a response button. Six subjects responded with their right index finger and the other six with their left index finger. In a block, the order of stimulus types was randomized, and subjects were asked to blink as few as possible and to maintain fixation on a small point presented at zero disparity and at the center of the monitor. Subjects took a short break between blocks.

2.4. EEG recording and data analysis

EEG was continuously recorded from 28 scalp electrodes that were mounted on an elastic cap according to the 10–20 system, including F7, F3, Fz, F4, F8, FT7, FC3, FCz, FC4, FT8, T7, C3, Cz, C4, T8, TP7, CP3, CPz, CP4, TP8, P7, P3, Pz, P4, P8, O1, Oz and O2. The electrode at the right mastoid was used as reference. Electrode impedance was kept below 5 kΩ. Eye blinks and vertical eye movement were monitored with electrodes located above and below the left eye. Horizontal electro-oculogram (EOG) was recorded from electrodes placed 1.5 cm lateral to the left and right external canthi. EEG was amplified with a gain of 500 K, bandpass filtered at 0.05–100 Hz. and digitized at a sampling rate of 1000 Hz. EEG epochs beginning 200 ms before stimulus onset and continuing for 700 ms were made. They were referenced off-line to a common average reference and selectively averaged according to stimulus type (Rossion et al., 2000). Those epochs contaminated by eye blinks, eye movements, or muscle potentials exceeding ±50 μV at any electrode were excluded from the average. The average waveforms were low pass filtered at 30 Hz and baseline corrected with respect to the mean voltage of the 200 ms pre-stimulus interval. Latencies were measured relative to stimulus onset. Topographic maps were computed for each stimulus type.

When assessing differences between two ERP waveforms, we have adopted a criterion of at least 28 consecutive samples (i.e. 28 ms) which are different at a $p < 0.01$ level (paired t-test for difference of means). Using the method proposed by Guthrie and Buchwald (1991), we calculated the corrected p-value of less than 0.017 (data sampled between 50 and 398 ms after stimulus onset). A similar, but less strict, criterion was used by Johnson and Olshausen (2005).

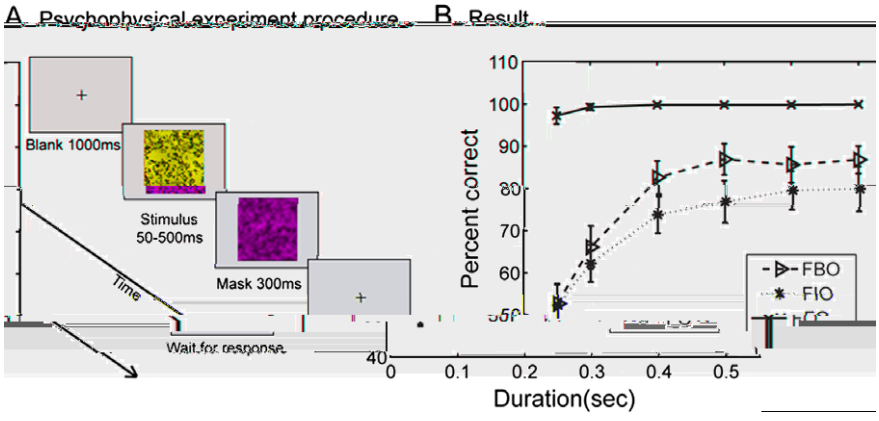

Fig. 2. (A) Schematic description of the psychophysical experiment. A face stimulus (FIO, FBO or FO) was presented with duration of 50, 100, 200, 300, 400 or 500 ms, followed by a 300 ms mask. Subjects were asked to make a judgment of the view direction of the face stimulus, either left or right and (B) psychophysical results. The performance of view direction judgment was plotted as a function of stimulus duration for the FIO, FBO and FO stimuli. Error bars denote one SEM calculated across subjects.

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3. Results

3.1. Psychophysical results

Subjects' performance of view direction judgment was plotted as a function of stimulus duration for the FIO, FBO and FO stimuli, respectively (Fig. 2B). For the FO stimulus, subjects had no difficulty judging the view direction of a face at all durations. Even with only 50 ms exposure, their performance could reach 97%. For the FIO and FBO stimuli, subjects' performance improved as the stimulus duration increased, but their overall performance significantly dropped down, compared to the FO stimulus. A repeated-measures analysis of variance (ANOVA) of percent correct was performed with stimulus type and duration as within-subject factors. Both the main effects of stimulus type ($F(2,12) = 144.768$, $p < 0.001$) and duration ($F(5,30) = 82.635$, $p < 0.001$) were significant, which were consistent with our observation.

To reveal the time course of amodal completion, we took a close look at the performance in the FIO and FBO conditions and their difference. The performance in the FBO condition, compared to the FIO condition, can be taken as a measure of amodal completion. When the performance in the FBO condition is better than that in the FIO condition, we attribute this to amodal completion. When the performance in the FBO condition is no better than that in the FIO condition, we take this to mean that amodal completion has not occurred. The extent of amodal completion as a function of stimulus duration was measured and defined as the time course of amodal completion (Murray et al., 2001). At shorter durations, there was no significant difference between the FIO and FBO stimuli (50 ms: $t(6) = 0.141$, $p = 0.893$; 100 ms: $t(6) = 1.754$, $p = 0.130$). At longer durations, subjects performed significantly better for the FBO stimulus than for the FIO stimulus (200 ms: $t(6) = 4.385$, $p = 0.005$; 300 ms: $t(6) = 4.153$, $p = 0.006$; 400 ms: $t(6) = 2.189$, $p = 0.071$; 500 ms: $t(6) = 2.863$, $p = 0.029$. Note that, at 400 ms, the effect was marginally significant). In other words, the performance functions for the FIO and FBO stimuli diverged after 100 ms, which suggested that the amodal completion started to manifest its effect after 100 ms.

To investigate the asymptotic characteristic of the performance function, we also run multiple paired t-tests to compare different duration conditions for the FBO and FIO stimuli, respectively, including 50 ms vs. 100 ms, 100 ms vs. 200 ms, 200 ms vs. 300 ms, 300 ms vs. 400 ms, 400 ms vs. 500 ms. For the FIO stimulus, the performance function increased from 50 to 200 ms, and then became saturated. This increase might be attributed to that a longer exposure (up to 200 ms) allow the visual system to scrutinize the face fragments for making judgments based on local features. For the FBO stimulus, the performance function increased from 50 to 300 ms, and then became saturated. The continued increase from 200 to 300 ms, relative to the FIO condition, suggested that the amodal completion still took effect after 200 ms, but terminated before 300 ms.

3.2. ERP results

Grand averaged ERPs over all subjects induced by the FBO, FIO and FO stimuli are shown in Fig. 3. For the FO stimulus, it induced

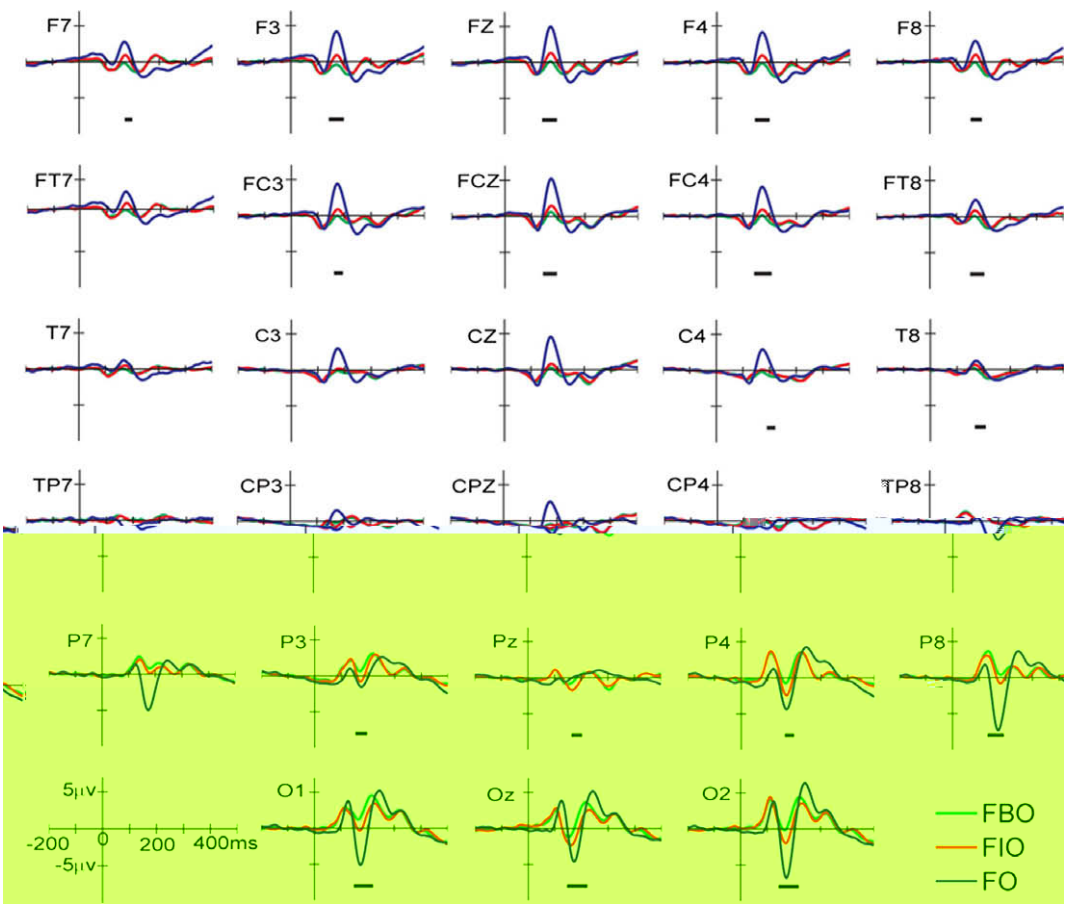

Fig. 3. Grand averaged ERPs induced by the FBO, FIO and FO stimuli. Black line at the bottom of each panel indicates timepoints which result in a statistically significant difference between the FBO and FIO conditions ($p < 0.01$, paired t-test).

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two face-sensitive ERP components – P190 at frontocentral scalp locations and N170 at posterior scalp locations (Joyce & Rossion, 2005). The amplitude of N170 showed right hemisphere dominance, which was consistent with previous studies (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Yovel, Levy, Grabowecky, & Paller, 2003). For the FBO and FIO stimuli, the amplitudes of both P190 and N170 were significantly diminished.

Since the psychophysical results suggested that the amodal completion took place between 100 and 300 ms after the stimulus onset by comparing the FBO and FIO conditions, we focused on the differential activity between the FBO and FIO conditions. Significant differences were found at 18 electrodes, including F7, F3, Fz, F4, F8, FC3, FCz, FC4, FT8, C4, T8, P3, Pz, P4, P8, O1, Oz and O2 (Fig. 3). Black lines at the bottom of each panel in Fig. 3 indicates the timepoints which resulted in a statistically significant difference between the FBO and FIO conditions ($p < 0.01$, paired t-test at 28 consecutive timepoints). The ranges of these timepoints at different electrodes are listed in Table 1. The earliest and latest timepoints of there ranges were 131 and 221 ms after stimulus onset, which fell into the range of the amodal completion (between 100 and 300 ms) measured by the psychophysical experiment. The progression of voltage topography from 131 to 221 ms for the difference wave (FBO minus FIO) is shown in Fig. 4A, with a general distribution of positive voltages at the posterior locations and negative voltages at the anterior locations. During the earliest stage of the difference, it was distributed at lateral parietal electrodes, and then gradually emerged at frontal and occipital electrodes. The earliest difference (131 ms) occurred at P8, which led other locations by at least 10 ms (Fig. 4

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locations, but also at temporal and frontal scalp locations. They mainly reflected the differential amplitudes of P190 and N170 to the FIO and FBO stimuli, and showed a right hemisphere advantage. Yovel and colleagues (2008) have demonstrated that N170 is closely correlated with the fMRI signals in the face-selective areas – FFA and STS. Thus, the overall evidence suggests that the ERP differences are the neural correlate of the amodal completion, which is somewhat face-specific. Also, the earliest ERP difference was found at P8, a scalp location situated immediately above STS, which implied the face-selective area played a pivotal role in the face amodal completion.

One of the long standing controversies regarding the neural mechanisms of amodal completion is whether amodal completion is a bottom–up, feedforward process or it relies on feedbacks from high-level cortical areas. Evidence supporting the former view comes from monkey neurophysiological studies that show early visual cortical areas (V1 and V2) responded to amodally completed shapes (Bakin, Nakayama, & Gilbert, 2000; Sugita, 1999; Zhou, Friedman, & von der Heydt, 2000). On the other hand, with methods of high-density electrical mapping and inverse source estimation, Murray et al. (2004) showed that the earliest sensitivity to amodal completion was found in LOC and V1/V2 responses to amodal completion likely reflect LOC feedback modulation. In our study, the ERP difference between the FBO and FIO stimuli was found between 131 and 221 ms after stimulus onset, with the earliest difference at P8 that led other electrode locations by at least 10 ms. It has been demonstrated that the initial feedforward sweep of processing in the macaque brain and presumably also in human brain is approximately completed around 100–120 ms after stimulus onset (Lamme & Roelfsema, 2000; Schmolesky et al., 1998). Thus, our data implied that amodal completion first manifested in face-selective areas and was implemented through feedback and recurrent processing among different cortical areas.

Using MEG and a similar stereoscopic depth manipulation, Harris and Aguirre (2008) did not find the effect of face amodal completion on the face-selective components – M170 and M400. In addition to the method difference (MEG vs. EEG), the perceptual contrast between the FBO and FIO stimuli in our study seems to be greater than that in Harris and Aguirre's study since we used randomly positioned and irregular holes that made the perceptual grouping of face fragments much more difficult. It is possible that the time course of the face amodal completion in their study is shorter than ours. Thus, data analysis focusing on M170 and M400 might have missed some earlier difference (e.g. M100) (Liu, Harris, & Kanwisher, 2002). It is worthwhile to perform psychophysical experiments and more detailed analyses to test this hypothesis.

In the ERP data, it is notable that, although the FBO stimulus can be perceived as a face better than the FIO stimulus, the face-selective components – P190 and N170 evoked by the FIO stimulus have larger amplitude than those by the FBO stimulus. Here are two possible interpretations. One is that this phenomenon might reflect a more difficult encoding of the FIO stimulus than of the FBO stimulus. A similar interpretation has been proposed by Rossion et al. (1999) to explain that the N170 elicited by inverted faces is significantly larger than that elicited by upright faces. The other interpretation is that isolated face components (e.g. eye) could elicit an N170 significantly larger than that elicited by full faces (Bentin et al., 1996). In the FIO stimulus, face components were perceived to be isolated and disjointed, which might have enhanced the N170 amplitude.

To conclude, our study measured the psychophysical and electrophysiological time courses of face amodal completion and provided further evidence regarding the representational development of occluded faces from local facial features to a coherent face. Future work combining fMRI and EEG/MEG is necessary to determine exactly how the development is actualized in the hierarchy of visual system.

Acknowledgments

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References

Bakin, J. S., Nakayama, K., & Gilbert, C. D. (2000). Visual responses in monkey areas V1 and V2 to three-dimensional surface configurations. *The Journal of Neuroscience, 20*(21), 8188–8198.

Bentin, S., Allison, T., Puce, A., Perez, E., & McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience, 8*(6), 551–565.

Fang, F., & He, S. (2005). Viewer-centered object representation in the human visual system revealed by viewpoint aftereffect. *Neuron, 45*, 793–800.

Grill-Spector, K., Kourtzi, Z., & Kanwisher, N. (2001). The lateral occipital complex and its role in object recognition. *Vision Research, 41*, 1409–1422.

Guthrie, D., & Buchwald, J. S. (1991). Significance testing of difference potentials. *Psychophysiology, 28*, 240–244.

Harris, A. M., & Aguirre, G. K. (2008). The effects of parts, wholes, and familiarity on face-selective responses in MEG. *Journal of Vision, 8*(10):4, 1–12..

Haxby, J. V., Hoffman, E. A., & Gobbini, M. I. (2000). The distributed human neural system for face perception. *Trends in Cognitive Sciences, 4*, 223–233.

He, Z. J., & Nakayama, K. (1994). Perceiving textures: Beyond filtering. *Vision Research, 34*(2), 151–162.

Hegdé, J., Fang, F., Murray, S. O., & Kersten, D. (2008). Preferential responses to occluded objects in the human visual cortex. *Journal of Vision, 8*(4), 1–16.

Hou, F., Lu, H., Zhou, Y., & Liu, Z. (2006). Amodal completion impairs stereoacuity discrimination. *Vision Research, 46*, 2061–2068.

Johnson, J. S., & Olshausen, B. A. (2005). The recognition of partially visible natural objects in the presence and absence of their occluders. *Vision Research, 45*, 3262–3276.

Joyce, C., & Rossion, B. (2005). The face-sensitive N170 and VPP components manifest the same brain processes: The effect of reference electrode site. *Clinical Neurophysiology, 116*, 2613–2631.

Kanwisher, N., & Yovel, G. (2006). The fusiform face area: A cortical region specialized for the perception of faces. *Philosophical Transactions of the Royal Society, B, 361*, 2109–2128.

Lamme, V. A. F., & Roelfsema, P. R. (2000). The distinct modes of vision offered by feedforward and recurrent processing. *Trends in Neurosciences, 23*, 571–579.

Liu, J., Harris, A., & Kanwisher, N. (2002). Stages of processing in face perception: An MEG study. *Nature Neuroscience, 5*, 910–916.

Michotte, A., Thines, G., & Crabbe, G. (1964). Amodal completion of perceptual structures. In G. Thines, A. Costall, & G. Butterworth (Eds.), *Michotte's experimental phenomenology of perception* (pp. 140–167). Hillsdale, New Jersey: Lawrence Erlbaum Associates Publishers (published 1991).

Murray, M. M., Foxe, D. M., Javitt, D. C., & Foxe, J. J. (2004). Setting boundaries: Brain dynamics of modal and amodal illusory shape completion in humans. *The Journal of Neuroscience, 24*(31), 6898–6903.

Murray, R. F., Sekuler, A. B., & Bennett, P. J. (2001). Time course of amodal completion revealed by a shape discrimination task. *Psychonomic Bulletin & Review, 8*, 713–720.

Nakayama, K., Shimojo, S., & Silverman, G. H. (1989). Stereoscopic depth: It's relation to image segmentation grouping, and the recognition of occluded objects. *Perception, 18*, 55–68.

Rauschenberger, R., & Yantis, S. (2001). Masking unveils pre-amodal completion representation in visual search. *Nature, 410*(15), 369–372.

Ringach, D. L., & Shapley, R. (1996). Spatial and temporal properties of illusory contours and amodal boundary completion. *Vision Research, 36*, 3037–3050.

Rossion, B., Delvenne, J. F., Debatisse, D., Goffaux, V., Bruyer, R., Crommelinck, M., et al. (1999). Spatio-temporal localization of the face inversion effect: An event-related potentials study. *Biological Psychology, 50*, 173–189.

Rossion, B., Gauthier, I., Tarr, M. J., Despland, P., Bruyer, R., Linotte, S., et al. (2000). The N170 occipitotemporal component is delayed and enhanced to inverted faces but not to inverted objects: An electrophysiological account of face-specific processes in human brain. *NeuroReport, 11*, 69–74.

Schmolesky, M. T., Wang, Y., Hanes, D. P., Thompson, K. G., Leutgeb, S., Schall, J. D., et al. (1998). Signal timing across the macaque visual system. *Journal of Neurophysiology, 79*, 3272–3278.

Sekuler, A. B., & Palmer, S. E. (1992). Perception of partly occluded objects: A microgenetic analysis. *Journal of Experimental Psychology: General, 121*(1), 95–111.

Shore, D. I., & Enns, J. T. (1997). Shape completion time depends on the size of the occluded region. *Journal of Experimental Psychology: Human Perception and Performance, 23*, 980–998.

Stone, L. S., Beutter, B. R., & Lorenceau, J. (2000). Visual motion integration for perception and pursuit. *Perception, 29*, 771–787.

Sugita, Y. (1999). Grouping of image fragments in primary visual cortex. *Nature, 401*(16), 269–272.

Author's personal copy

Tarr, M. J., & Cheng, Y. D. (2003). Learning to see faces and objects. *Trends in Cognitive Sciences, 7*, 23–30.

Weisstein, N., Montalvo, F. S., & Ozog, G. (1972). Differential adaptation to gratings blocked by cubes and gratings blocked by hexagons: A test of the neural symbolic activity hypothesis. *Psychonomic Science, 27*, 89–91.

Yovel, G., Levy, J., Grabowecky, M., & Paller, K. A. (2003). Neural correlates of the left-visual-field superiority in face perception appear at multiple stages of face processing. *Journal of Cognitive Neuroscience, 15*(3), 462–474.

Yovel, G., Sadeh, B., Podlipsky, I., Hendler, T., & Zhdanov, A. (2008). The face-selective ERP component (N170) is correlated with the face-selective areas in the fusiform gyrus (FFA) and the superior temporal sulcus (fSTS) but not the occipital face area (OFA): A simultaneous fMRI-EEG study. *Journal of Vision, 8*(6), 401.

Zhou, H., Friedman, H. S., & von der Heydt, R. (2000). Coding of border ownership in monkey visual cortex. *Journal of Neuroscience, 20*, 6594–6611.